

REPRODUCTIVE BIOLOGY OF THE MUGGER (*CROCODYLUS PALUSTRIS*)¹

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(With two plates & five text-figures)

Mugger (*Crocodylus palustris*) were studied in the wild at locations in India and Sri Lanka and in captivity in Madras. Mugger range from Iran east to Assam in India and south to Sri Lanka; they have been exterminated throughout most of their range.

Mugger are adaptable and occupy a wide range of habitats, including streams, rivers, lakes and saline lagoons. Basking is an important daily activity and was noted to decrease in the hot season or when a strong breeze was blowing. Mugger have developed two main strategies to survive their highly seasonal environments: tunnelling and overland travel. They are strong swimmers and use the high walk and belly run for terrestrial locomotion.

Mugger can be fast when catching prey; hatchlings were observed jumping to catch flying insects and captive adults caught wild monkeys, crows and kites. In some localities they are mainly fish eaters. Other prey items include beetles, rats, snakes and frogs. Man eating is rare, the Sri Lanka race receiving most credit for this habit. Gastroliths were often found in mugger stomachs through their function, if any, remains unknown. Mugger have acute senses of sight, hearing and smell.

Hatchling mugger averaged 27 cms in total length; the maximum recorded length for the species was 5.63 m. A captive-reared female of 2.20 m bred at 6 years 8 months.

November to June is the breeding season in South India and a month later in the north. Mugger are fairly tolerant of conspecifics. Prominent social signals by the male included head slapping, chasing, tail up swimming, geysering and bellowing. Females defended nest sites by tail thrashing and chasing. Submission was signalled by raising the head.

During courtship circling, bubbling and jaw touching preceded copulation. Females lay an average of 25-30 eggs in holes within 10 metres of the water incubation averages 66 days. Double clutching was observed for 5 years in captive mugger in Madras. Nest defence, hatching, release and transport of young was observed in captivity. Defence of hatchlings was observed in both sexes. Conservation included egg collection, rearing and release.

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INTRODUCTION

By the time formal studies were started on this crocodile the mugger (*Crocodylus palustris*) had been exterminated throughout most of its range (Whitaker and Daniel 1978).

Only small, remnant populations remain. In parts of Sri Lanka however the mugger can still be found in concentrations of 100 or more in a single tank (man made lake) (Whitaker and Whitaker 1979).

Till the 1970's the only scientific reports on the species were miscellaneous notes mainly in the Journal of the Bombay Natural History Society. McCann (1940) and D'Abreu (1915) made some of the first observations on breeding and feeding habits of mugger, and M. A. Smith (1927, 1935) did the first major work on its systematics and distribution. P. E. P. Deraniyagala made the first systematic effort to formally record data on the mugger's taxonomy and embryology (1936, 1939).

Yadav (1969) and David (1970) reported on captive breeding of the mugger. In the early 1970's mugger were housed at the Madras Snake Park (MSP) and later (1974) as a breeding group of the then established Madras Crocodile Bank (MCB). What little we know of the behaviour of the mugger is based mainly on observations of captive animals. Parker (1880) and Dharmakumar-sinhji (1947) published the first notes on wild mugger breeding behaviour. An account of captive breeding behaviour was made by Whitaker and Whitaker (1977 a, b).

Other literature on the mugger includes references on where and how to shoot them (for example Shortt 1921) and status survey reports for N. E. India (Biswas 1970), South India, Gujarat (Whitaker 1974, 1977) and Sri Lanka (Whitaker and Whitaker 1979). The Govt. of India/UNDP/FAO crocodilian rehabilitation programme is undertaking several studies of the mugger, publications on which are anticipated.

This treatment of mugger biology outlines current knowledge of their distribution, status, habits and conservation and concentrates on

reporting results of our studies on the breeding biology of the species.

MATERIALS AND METHODS

Studies on wild crocodiles

We have been involved in the survey, study and captive breeding of mugger in India since 1970. Day and night census was carried out in Tamil Nadu, Karnataka, Gujarat States, Sri Lanka and western Nepal. Prolonged observations were made in Corbett National Park, Uttar Pradesh, North India. Wild egg collection was undertaken in Tamil Nadu and Gujarat.

Captive facility

Captive mugger have bred for seven years in Madras, South India. At MSP, a breeding pair resides in a 310 m² walled enclosure. The 18 m² concrete pond is surrounded by natural scrub. The soil is laterite, hard and pebbly. The present breeding group of 12 adults (4 males, 8 females) at MCB is housed in a large (1780 m²) walled and naturally landscaped enclosure which is planted with common coastal vegetation (*Casuarina*, *Pandanus*, grasses). The pond is an excavation filled by the natural aquifer, varying in area from 600 to 1200 m² and 1-2.5 m in depth in the dry and wet seasons. The substrate is sea sand and temperatures, rainfall and feed the same as at MSP. 900 juveniles and subadults are also being reared at MCB. Data from these animals has provided much of the information reported herein. Mugger at both facilities are fed rats, frogs, fish and beef. In Madras, rain is confined mainly to the northeast monsoon (October-December) with an annual average of 1200 mm. Shade temperatures throughout the year range from 20° to 45° C.

RESULTS AND DISCUSSION

Distribution

Mugger are found from the Sarbaz River in southeastern Iran east to Assam and south to Sri Lanka (Honegger 1971). The validity of a single record of a mugger in Thayetmyo, Burma (Annandale 1921) is doubted by M. A. Smith (1927). The species occupies a variety of habitats and was apparently once very common in many parts of its range (Shortt 1921, Deraniyagala 1939). In Sri Lanka, a single specimen was reported at Kandy, 450 m. above sea level (Whitaker and Whitaker 1979) and in India the highest confirmed record is at Corbett Park, 420 m. above sea level.

Status

The species is regarded as endangered; exterminated in most of its range, rare in Iran, and near extinction in Pakistan (Webb 1978). It is listed in the IUCN Red Data Book and is on Appendix I of the Convention on International Trade in Endangered Species. Mugger are protected by law in all the countries of their occurrence.

The once large population of captive mugger at Mugger Pir in Pakistan has dwindled to three adults (H. W. Campbell, pers. comm.). The two largest known concentrations of the species on the Indian subcontinent are at Amaravathi Reservoir, Tamil Nadu State with about 14 adults and Hiran Lake, Gujarat State, with about 50 adults.

Habitat

Though named *palustris* (swamp dwelling), mugger are mainly river and lake dwellers, adjusting to a wide range of habitats. We have encountered mugger in diverse habitats including hill streams, large man-

made reservoirs, annual tanks, large rivers, small jungle pools, irrigation channels and saltwater lagoons. Habitat preference may be limited by their hole nesting habits. Carr (1963) proposed that mound nesting would appear an adaptation to swampland by truly palustrine species such as *Crocodylus novae-guineae* and *Alligator mississippiensis*. In fact the Indian mainland has relatively little freshwater swamp habitat. The present day largest populations of mugger are found in the annual tanks of the 'dry zones' of Sri Lanka; only here do they approach what might be called original concentrations. Deraniyagala (1936, 1939) notes that mugger in Sri Lanka are found mainly in lowland rivers, lakes, forest pools and, remarkably, in the salt pans and associated lagoons.

On the Indian sub-continent mugger have been recorded in the salt lakes near Thatta in the Sind (McCann 1940). Bustard (1974) notes their "adaptability to village and irrigation tanks in addition to rivers, swamps and lakes." He also writes that much of their habitat has been "affected by dam construction" as in Sri Lanka where natural habitat has been altered by thousands of miles of canals and channels. Sometimes however these modifications are beneficial to crocodiles, offering alternate habitat, hunting grounds and access to other tanks (Whitaker and Whitaker 1979).

DAILY ACTIVITY

Amphibious behaviour

During the 1977/78 breeding season (December-January) ZW made 55 hours of behavioural observations on the mugger breeding group at MCB. Observations were made from a hide in the enclosure, generally during the most active period, i.e. early

morning and late evening. Activities of seven mugger were recorded during a week in mid-January. Table 1 shows the percentage of time spent at each activity. Most crocodiles spent over half their time stationary in the water though the dominant female (Nova) spent more time on the bank. The dominant male (Perayur) spent more time swimming than the others. The 4 sub-dominant females were the least active of all. During the hot season (April-July) the MCB mugger spend most of the day under water and only emerged onto the bank during the night.

April, mugger typically moved onto land from 7 a.m. (air temperature 18-21° C) till noon (35-39° C). No further emergence occurred till well after sunset when the largest mugger (over 3 m.) would emerge on to the rocks (Whitaker 1979 b).

Burrowing, aestivation and seasonal movement

Writing of mugger in the northern peninsula of Sri Lanka Baldeus (1671) related, "In Jafnapatnam there are many crocodiles in the fens, ponds, and lakes, which if they happen to dry up in the summer, they dig holes to live in" Later Deraniyagala (1936) writes that the mugger "often excavates bur-

TABLE 1

DAILY ACTIVITY OF CAPTIVE MUGGER IN SOUTH INDIA (MCB) DURING A WEEK (MID-JANUARY) IN THE BREEDING PERIOD (% OF TIME SPENT)

Crocodile age (years) / length (cms)	Partly or fully on bank	Stationary in water	Swimming	Courtship	Other social interaction	Underwater
Perayur (Beta) male/19 (282)	28.2	57.7	7.0	1.4	—	5.6
Nova (Alpha) female/17 (200)	52.1	41.1	2.7	1.4	—	2.7
Metty female/7 (270)	35.3	61.8	2.9	—	—	—
4 females 6-9 / (152-188)	19.7	78.8	1.5	0.08	—	—
Average	33.8	59.8	3.5	0.96	—	4.1

At Vakkaramari Waterworks in mid-May, adult mugger took an average of two hours (0600-0800) to gradually reach shore before emerging onto land. Then, they spent an average of 3½ to 4 hours on shore. Afternoon emergence was rare, probably because of a daily brisk northwest breeze (Whitaker 1974). At MCB a similar schedule has been observed; diurnal basking is significantly less in the hot season, when the crocodiles spend most of the day submerged. At Corbett National Park in

rows in the bank." In the salt lakes near Thatta in the Sind (Pakistan), mugger were observed occupying burrows on the hills bordering the lake. The holes were about 60 cm in diameter and 2.5 to 4.5 m. deep, ending in a chamber wide enough for the crocodile to turn around in (McCann 1940).

In South India two burrows of about 0.75 m diameter and 2.5 m. deep were seen at Kilikudi, Tamil Nadu and described "perhaps as a hot season refuge" (Whitaker 1974).

In Kedarhalla stream, burrows up to 6 m. deep under the supportive root systems of trees (e.g. *Eugenia jambolana*) on the banks are the only refuges for the mugger there during the prolonged dry season (Whitaker and Whitaker 1976). One was horse-shoe shaped with two openings. We saw similar burrows in stream banks on the Menik Ganga river near Kataragama in Sri Lanka and in the Gir Forest, Gujarat. At Hiran Lake in the Gir National Park, 16 burrows, all with flattened openings, averaging 80 cms in width, 4-5 m. deep and almost every one containing a mugger were observed on a steep embankment. Some of the holes were at water level, and some 3 m. up the bank (Whitaker 1977). In southern Sri Lanka a mugger resided in a burrow dug in the sand bank of a saltwater lagoon (Whitaker and Whitaker 1979). After several abortive attempts, a 3 m. male mugger at MCB excavated a burrow under the overhanging roots of several *Casuarina* trees in the mugger breeding pen.

Burrowing has been observed in yearling, subadult and adult mugger at MCB. Burrowing seems to be a survival tactic in mugger to withstand the drought conditions which are a standard feature of the dry season in many parts of the range. However in some situations mugger although they frequent the water, appear to reside permanently in burrows, emerging to bask by day and hunt at night.

An adult MCB female mugger 'Metty' was observed several times while burrowing. Inserting her head under the tree roots she would dig with front feet and propel the sand back with the hind feet, dispersing sand with swimming movements of the tail. The dominant female in the pen would often use the tunnel (which was located close to her nest site) with no

apparent objection on the part of the Metty. In the wild in India only one mugger was observed per tunnel although at the Menik Ganga study site, it was thought that many of the mugger observed at night resided in the 3 tunnels located (Whitaker and Whitaker 1979). It seems likely that mugger will group together in a single tunnel as observed in the Nile crocodile (Guggisberg 1972).

Overland travel by mugger is well documented. In India they travel overland at night to the nearest tank when the water dries in summer (Ahmed 1945). In Sri Lanka, trans-tank migration is a yearly phenomenon during the dry season (Whitaker and Whitaker 1979). In the Barda Hills, Gujarat, at least 50 crocodiles were reported to have left a reservoir as the dry season progressed. The trail of one subadult was followed for about 2½ kms through steep, hot scrub jungle. The animal was found under a sheltering overhanging rock 6 kms from the next tank (Whitaker 1977). This is not a random movement.

Overland travel is a likely mode of colonization particularly by subadult and juvenile mugger. Evidence of single crocodiles present in small hill streams above waterfalls at Kedarhalla and Amaravathi in Tamil Nadu demonstrates the tenacity of the species in seeking new habitat.

Locomotion

Like other crocodylians mugger use the powerful, laterally flattened tail to swim, using the webbed hind feet to stabilize when still, change direction and aid the 'reverse dive', a typical mode of submerging. Mugger often waik lightly on the bottom of a pond or river, using the same 'belly walk' as on land. Where there is a lot of marsh gas it

is easy to see the bubble trail of a bottom walking mugger.

Mugger have not been observed galloping, though the other modes of locomotion on land, the high walk and belly run recorded for the Nile crocodile (Cott 1961 a, b) are the same. Though not classed as a regular mode of locomotion, climbing has been observed in mugger of up to 2.8 m. In captivity adult mugger climbed over vertical chain link mesh fencing 1.75 m. high and small juveniles climbed up 80 cm rough cement walls at the corners. In the wild this ability based on limb and claw strength, is used by mugger in travelling steep terrain and climbing up to burrows many metres above drought water levels.

Feeding

Mugger are heavy set animals and appear sluggish, but are actually alert and capable of fast reaction and considerable speed in defence or when hunting. Hatchlings have been observed jumping to successfully snap at winged termites and moths attracted to a light over their pond.

Mugger are curious animals and will briefly investigate any movement in or near their habitat. If interested, mugger will submerge and reappear near the potential prey. Prey is caught with a sudden forward lunge or sideways snap. Captive adults at MSP and MCB have captured monkeys, crows and kites which entered the breeding enclosures.

Small prey is killed by a quick, crushing bite. Larger prey is shaken, drowned and/or dismembered as a limb (or head) is grabbed and twisted several times while the mugger rolls in the water using tail leverage.

In some localities mugger appear to be mainly fish eaters, particularly where intense dry seasons create high concentrations of fish.

Spittel (1924) writing about Sri Lanka, stated that "salt concentration causes a massive fish kill and crocodiles, birds and other scavengers feast."

The annual drying of most streams and tanks is characteristic of the geographical dry zones in the mugger's range. Large mugger establish themselves in the last remaining water, the essential focal point for a vast range of dependent animal life, and could probably survive the rest of the year on the dry month or two of super-abundance of prey.

Crocodiles were observed 'herding' fish to shore in the daytime at Hiran Lake, Gujarat and at night at Amaravathi Reservoir, catching them as they leapt in an attempt to escape from the shallows back to deep water. At MCB an adult female of 2.00 m. length was observed to purposefully herd fish after a 60 day fast during brooding. She gradually shifted her body perpendicular to the west finger of the breeding pond and slowly moved sideways, gradually reducing the enclosed end of the finger. Several bites in quick succession enabled her to catch a number of *Tilapia mossambica*. This behaviour has been observed in the wild in Nile crocodiles (Graham and Beard 1973) and the saltwater crocodile (*Crocodylus porosus*) (Whitaker, pers. obs.).

On two occasions at MSP a young adult male (2 m.) mugger was observed catching a live rat snake (*Ptyas mucosus*). Rather than killing the snake immediately at it would other prey, the crocodile shook it hard and dropped it and then repeated the process 3-4 times until the snake was motionless. The overall impression was that the mugger was hesitant with the snake.

Mugger being reared at the Gharial Rehabilitation Center in Orissa were fed pigeons which were stalked and adroitly caught (Singh 1979). In a river in Pakistan a mugger was

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observed catching an otter. A captive specimen at Mugger Pir near Karachi was seen to catch a peacock (Smoothbore 1877). Besides actively hunting, mugger apparently also forage for such sedentary food items as snails and bivalves (D'Abreu 1915; Whitaker, pers. obs.) and will locate and eat carrion (Champion 1934).

Stomach contents and feces examination

A 1.35 m. mugger taken from a forest pond contained 32 water beetles (*Cybister* sp.), 15 water bugs (*Belostoma* sp.) and 4 snail opercula (*Ampullaria* sp.); the stomach of a 3.24 m specimen contained 1 Indian bullfrog (*Rana tigrina*) (D'Abreu 1915). A specimen from Powai Lake, near Bombay contained 60 water beetles, 2 fish (*Chela* sp.) and an eel (McCann 1935). Brander (1927) lists animal remains which he found in mugger shot by him: men, leopards, wild dogs, hyaenas, spotted deer, sambar, nilgai, four horned antelope, barking deer, monkeys, domestic dogs, goats, calves, pigs, ducks, storks and other birds.

Fish scales, egret feathers and watersnake (*Xenochrophis piscator*) scales were found in a sample of feces at Hiran Lake, Gujarat State (Whitaker 1977). Sixty fecal pellets representing about 30 defecations were collected and examined at Vakkaramari, Tamil Nadu State. The results indicate selective hunting for rats during the dry season (May), when rats live near water.

Prey remains	% occurrence
Fish scales	10%
Rat hair (<i>Bandicota bengalensis</i>)	100%
Gerbil hair (<i>Tatera indica</i>)	20%
Snakes scales (<i>Xenochrophis piscator</i> and <i>Amphiesma stolata</i>)	10%
Bird feathers	10%

(Whitaker 1974).

In Sri Lanka, a random sample of mugger feces contained remains of fish, birds, wild pig (*Sus scrofa*) and Russell's viper (*Vipera russelli*).

Man-eating

It is likely that many of the reports of man-eating in mugger confuse mugger with salt-water crocodiles. It is also probable that attacks on humans are often cases of mistaken identity. Occasional attacks seem to have occurred and feeding on corpses was probably a commonplace event. Shortt (1921) describes the discovery of an entire corpse in a mugger. Often, when firewood for cremation is hard to come by, whole corpses are thrown into the river. It is likely that this is the source of ornaments found in mugger stomachs reported among others by Pitman (1913) and Battye (1944). In the present day it is common to see floating corpses on major north Indian rivers such as the Jumna and Ganga but it is now the dog packs that fatten on them, in the absence of mugger.

Deraniyagala (1936) unequivocally states that mugger in Sri Lanka will take humans as prey and in fact uses this habit as one of the criteria for calling it a sub-species separate from the Indian mugger. In 1977 a young village farmer who survived a mugger attack at a small stream in south-eastern Sri Lanka was interviewed by us. The crocodile was observed to be a 2 m. adult and this appeared to be a typical case of mis-predation (Whitaker and Whitaker 1979).

Gastroliths

While some authors suggest that the phenomenon of stone ingestion in crocodilians is an aid to digestion, Cott (1961, a, b) presents a case for the theory that gastroliths perform a hydrostatic function as ballast (a native be-

lief), the stones averaging 1% of the adult Nile crocodile's total weight. McCann (1940) suggests that the size of the stones is related to the size of the animal. A 3.42 m. mugger contained about 1 kg. of stones of assorted sizes (Simcox 1905). D'Abreu (1915) reports a 1.35 m. mugger having 16 small stomach stones and a 3.24 m. mugger with 6 large stones and 12 smaller ones. A 2.75 m. mugger found dead in Corbett National Park contained a few small pebbles and gravel in its stomach (Whitaker and Ross, unpubl.). A 3.12 m. mugger shot at Jasdan, Gujarat contained an unusually large gastrolith weighing 2.5 kgs (Dharmakumarsinhji 1952). A 3.27 m. mugger killed at the Krishnarajasagar Dam in Karnataka, South India contained 12 stomach stones of roughly 12.5 mm/diameter (Krishnamurthy 1951). Peaker (1969) observed a captive American alligator deliberately pick up and swallow pebbles of 1.5 cm diameter and describes the habit as "reminiscent of the situation in granivorous birds."

Senses

McCann (1940) notes that mugger have acute senses of sight, hearing and smell. This is supported by observations by us on captive and wild mugger. They were observed catching, moving and flying prey with great precision, demonstrating visual acuity. Wild mugger at most localities were extremely difficult to approach closer than several hundred metres; ears and eyes presumably being the important detecting devices. Mugger were observed searching for and locating prey objects on land and under water by 'feeling' with their jaws. A blind gharial (*Gavialis gangeticus*) was observed catching fish and locating dead fish, obviously by feel (Singh, pers. comm.). These observations lend support to Bellairs' (1969) suggestion that the tactile

TABLE 2

GROWTH RATE OF 12 MSP HATCHLING MUGGER

Age	Average total length (cms)	Length gain (cms)	Average weight (gms)	Weight gain (gms)
1 month	32.1	—	48.5	—
9 months	57.2	25.1	650.8	602.3

TABLE 3

GROWTH RATE OF 50 MCB HATCHLING MUGGER

Age	Average total length (cms)	Length gain (cms)
Hatching	28 (26-31)	—
12 months	82 (57-104)	54
24 months	130 (90-170)	48

(Whitaker and Whitaker 1977 b).

TABLE 4

DIFFERENTIAL GROWTH RATES IN MUGGER

Origin	N	Months	Growth rate (cms per month)
Ahmedabad Zoo, Gujarat	6	84	1.6
Kilikudi, Tamil Nadu	4	72	7.2
MCB (captive bred)	21	48	2.3
Kedarhalla, Tamil Nadu	7	60	2.5
Hogenakal, Tamil Nadu	13	60	2.7

organs in the scales of the jaws may be specialized for detecting disturbance under water created by fish.

Size, growth rate

Mugger are 25-30.5 cm (average 27 cm) in total length when they hatch. Table 2 demonstrates an average monthly length increase of 2.8 cm and an

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average monthly weight increment of 66.9 gm in 12 hatchlings for 9 months. Table 3 demonstrates increases in length of 4.25 cm per month in over 50 hatchlings for 24 months. Six hatchlings from wild collected eggs averaged 75 gms in weight at one month post hatchling and 32 months later averaged 10 kg, an increase of 310 gm per month (Whitaker 1974).

D'Abreu (1935) records a captive mugger growing from 27.5 cm to 210 cm in 19 years. An escaped mugger grew from 170 cm to 220 cm during 40 months in the wild, the only existing growth rate of a wild mugger (Acharjyo and Mohapatra 1977).

The maximum reliably recorded total length for the mugger is 5.63 m for 2 specimens killed at Kantalai Reservoir in Sri Lanka (Deraniyagala 1939). In recent years the average adult male size is 3 to 3.5 m and female 2 to 2.5 m.

Table 4 shows that mugger hatchlings of wild collected eggs and captive bred stock from

different localities grew at different rates, indicating population differences in growth rates. Variable growth rates of different populations have also been reported by Bustard (in litt.).

Sexual maturity

A captive reared, 11 year old 180 cm long female mugger bred at MSP. A captive reared 220 cm female at MCB bred at 6 years 8 months and a male mugger at MSP bred when 8-10 years old and 250 cm in length (Whitaker 1979 a). McCann (1940) examined the gonads of a 180 cm female mugger which had bred that season.

SOCIAL BEHAVIOUR AND REPRODUCTIVE BIOLOGY

Timing of breeding season

The breeding season of *Crocodylus palustris* (in this paper the period between and including courtship, mating, nesting and the hatch-

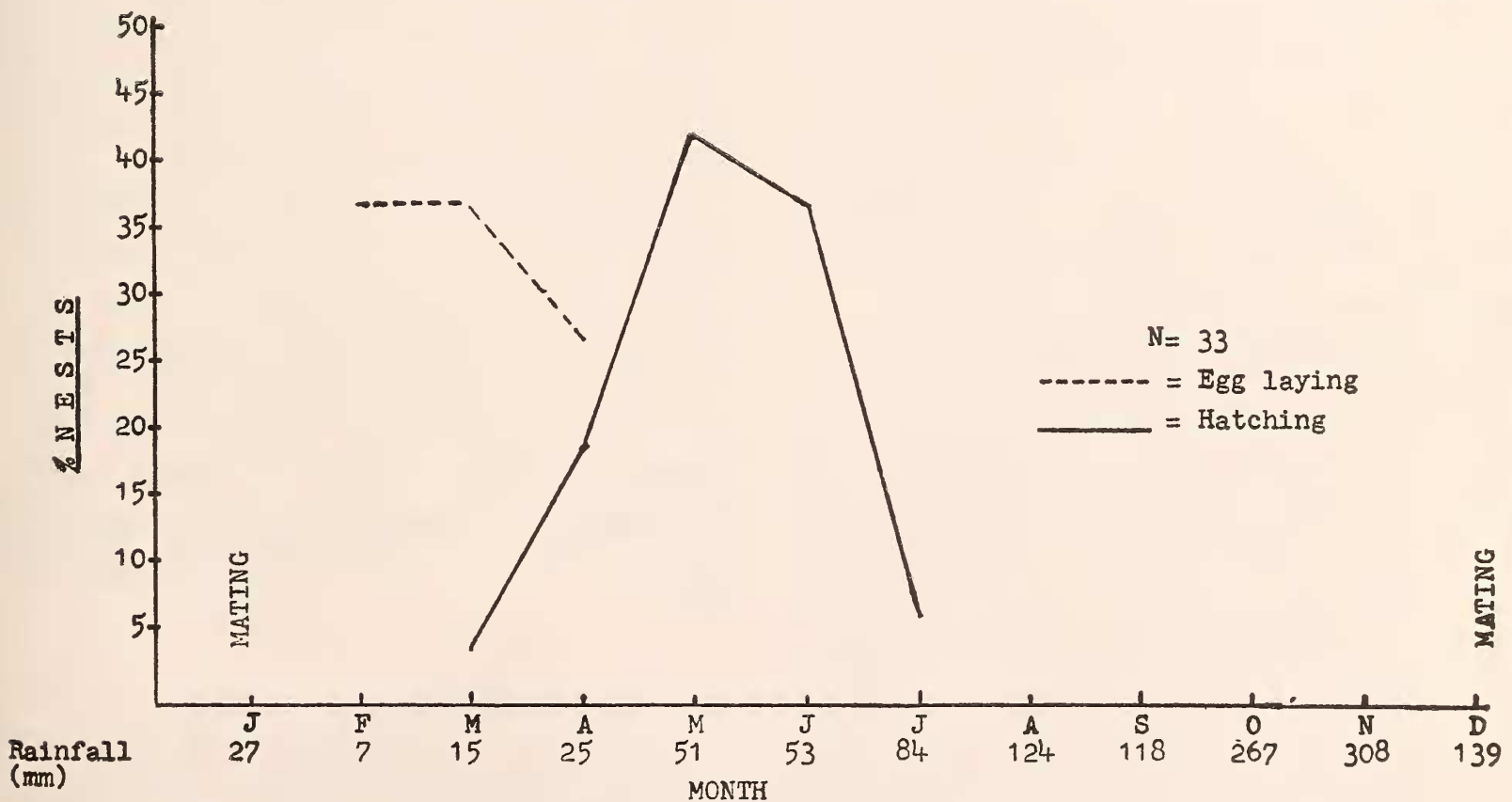


Fig. 1. Seasonability of mugger reproduction at Madras Crocodile Bank, South India.

ing of young) extends from November to June in South India. Courtship and mating coincide with the north-east monsoon, nesting with the beginning of the dry season, hatching with the height of the dry season and the beginning of the south-west monsoon. Courtship and mating commence in late-November-early December, nesting in February-April, hatching in April-June (Whitaker and Whitaker 1974, 1977 b) (see Figure 1). In northern India it tends to be one month later. In Jaipur, Rajasthan nesting is recorded for 9 May (Yadav 1969). At Jaipur Zoo from 1967-71, a female *C. palustris* nested between 25 April and 22 May, and hatching occurred between 26 June and 6 July (Prakash 1971). In Sri Lanka, June-July are reported as the laying months (Parker 1880) and August is given as a hatching date for mugger (Deraniyagala 1936) and later confirmed by Whitaker and Whitaker (1979).

Territoriality

Although fighting sometimes occurs on the introduction of a new individual in an established captive group, mugger are fairly tolerant of conspecifics, particularly during the seasonal concentrations which occur in the dry season. During the breeding (wet) season both sexes become increasingly territorial. At MCB, the largest male 'Beta' asserts his dominance by swimming displays in the 'tail up' position, head-slapping and chasing and biting subordinate males, sometimes on the shore. This behaviour has been recorded for males of other species as well, such as *C. novaeguineae* (Lang, in press) and *C. niloticus* (Modha 1967; Pooley 1976). D'Abreu (1915) notes that large wild mugger "usually" have shortened tails, some missing the terminal 9-10 segments. This is not the case with most wild mugger observed today and could be an

indication of much more frequent interaction among the adults of once large and concentrated populations.

Roaring or bellowing was rarely heard in mugger but it is reported in the literature; this vocalization could be a territorial signal. McCann (1940) reports that a 3 m. mugger shot in a hole roared like "the roll of a big drum". A 3.75 m. mugger on the Indravati River, Madhya Pradesh, bellowed 2 or 3 times in quick succession and is described as sounding like a cow bellowing (Battye 1944). In Sri Lanka a mugger bellowed in response to a rifle shot (Rossel 1944).

A raised, threatening posture, called 'slimming' by Garrick *et al.* (1978) was frequently observed in captive juveniles and subadult males. The animal raises its body by fully extending its legs, sometimes slightly compressing its body laterally and breathing deeply. This is occasionally initiated by the approach of another mugger to a favoured basking spot but also by apparent individual rivalry, perhaps an early mechanism of the establishment of social hierarchy. This posture is rarely used when confronted by an animal (or human), the most common threat used being a raised forebody with open mouth, hissing and leaping forward if cornered or further threatened. A challenged subdominant mugger of either sex may run or raise the head in submission, often accompanying the signal with a low, open-mouthed gurgling sound. Other behaviours observed in mugger which are possible social signals include 'yawning' (as described by Garrick *et al.* 1978) and 'ear flapping' (Bellairs 1969).

Courtship and mating

Observations on courtship and mating were made from a hide in the mugger breeding enclosure at MCB. Often a head slap by a male

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(which starts from the head up position) signalled approach and courtship. For example on March 9, 1978 at 0810 Beta head slapped, approached a female and mounted. The female submerged, Beta moved away; the female surfaced near his head, jaw raised. Male approach prior to courtship was usually in the tail-up position, with the single caudal crests arched well out or slightly out of the water. In one instance following a head slap geysering was observed as described by Garrick *et al.* (1978) — “a stream (spout) of water about 10 to 20 cm in height resulting from a release of air from the external nares while the snout is just under the surface of the water.” Beta was heard roaring as in Garrick *et al.* (1978) prior to a courtship sequence.

During courtship, circling, bubble blowing and raising and touching jaws was observed. On 18 January 1978 at 1017 (following a head slap) Beta swam to tank centre in the tail up position, nudging a female’s back with his

head. The female raised her jaw, circled, bubbled, submerged. Beta raised his jaw, hissed, submerged. Female raised her jaw, both submerged for 5 minutes. Figure 2 provides a summary of these behaviours.

Females were observed bubbling at times other than during mating. Bubbling is perhaps a female courtship signal. Sometimes it was associated with a cough. Female mugger occasionally head slapped, as do *A. mississippiensis* (Garrick *et al.* 1978) and were twice observed to roll over in the water, exposing the belly as reported by Cott (1961) for *C. niloticus*.

During a courtship sequence on 14 January 1978 from 0855 to 1010 am a female mugger was observed repeatedly mock biting (Garrick and Lang 1977) the male’s head. When the male mounted the female the pair submerged and mating progressed while fully or partially submerged, often surfacing and submerging alternately. Copulation lasted from five to fifteen minutes. During courtship and mating a high

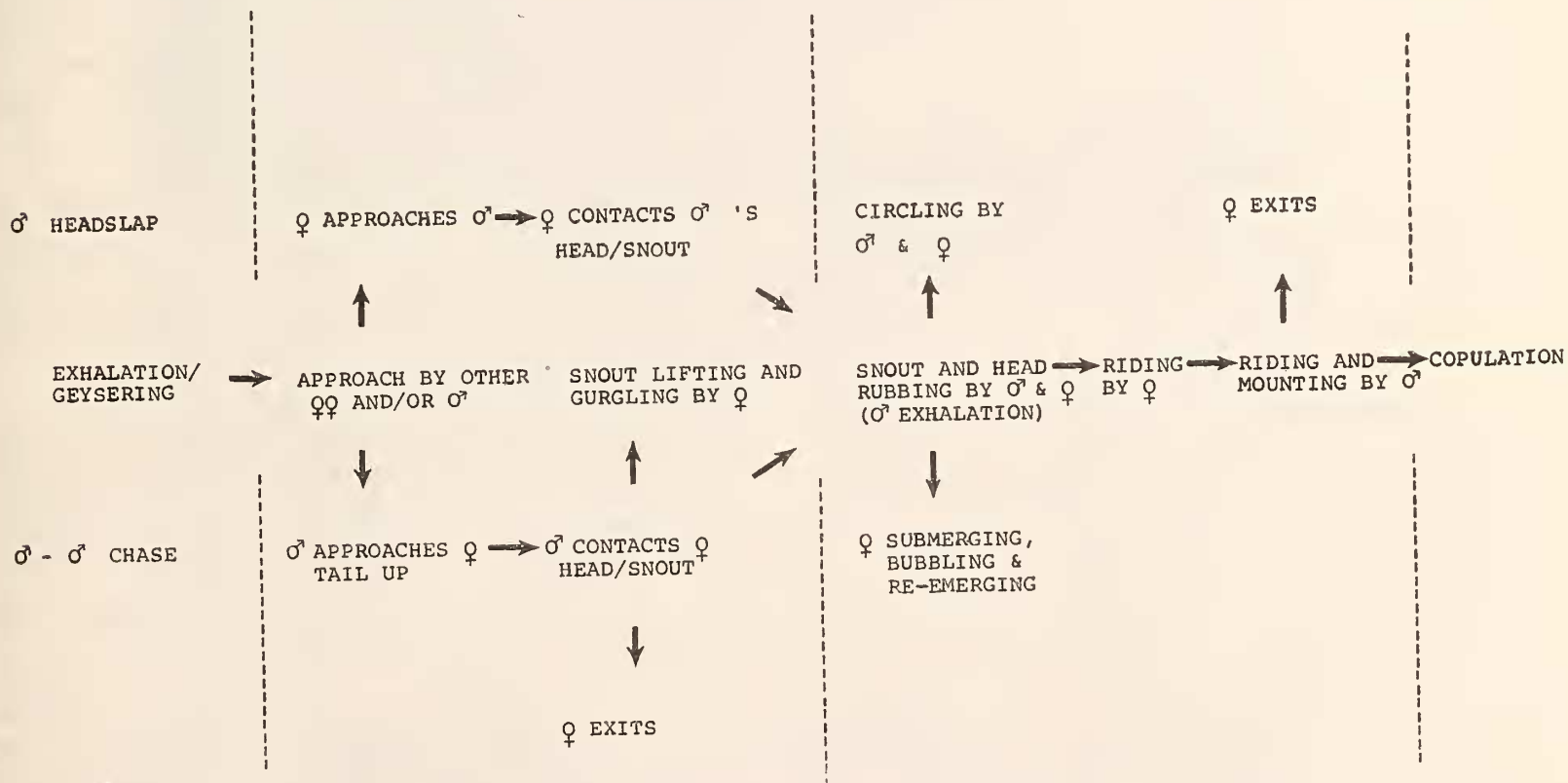


Fig. 2. Summary table of mugger reproductive behaviour as observed at Madras Crocodile Bank (after Garrick and Lang 1977).

degree of tolerance was shown toward other animals. Adult females and a sub-adult male were seen circling, nudging and in intermittent physical contact with a pair during courtship on several occasions. Courtship and mating were always observed in water though Yadav (1969) records copulation on dry land at the Jaipur Zoological Gardens.

On several occasions during courtship the throat glands of females in the head raised posture were briefly everted and withdrawn. It is possible that the scent glands function in some stimulatory capacity during pre-mating courtship. Prater (1933) reports that the scent glands in the throat and vent secrete a brownish liquid with a musty odour. He feels that the secretion is most active during the mating season and postulates that its release in the water enables individuals to find each other. This secretion has been observed as a waxy brown substance but seems to have very little detectable odour.

Dharmakumarsinhji (1947) made the first observations on breeding of wild mugger. He described the tail up and head emergent posture of the male and head up posture of the female prior to copulation. His observations agree with those of the authors, including the submerging, re-emerging cycle seen during copulation.

Nest construction and egg laying

Nesting females were observed at MCB. On 14 February 1979 on arrival at the breeding enclosure at 2100 a 7½ year old female was seen lying on her freshly dug nest. At 2130 p.m. an egg (the last of her clutch) was expelled with a prolonged grunt. After laying the female inserted both feet into the egg chamber and gently pushed the entire clutch to the back of the cavity of the L-shaped hole (Figure 3). For this manoeuvre and while nest

packing the tail was used for support (Whitaker 1979 c). She then began a slow

Crocodylus palustris EGG PLACEMENT WITHIN NEST

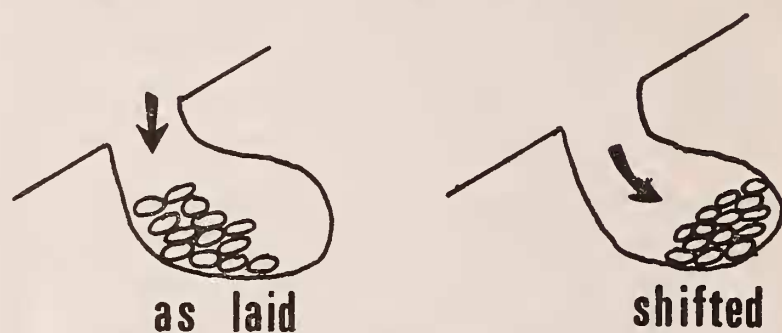
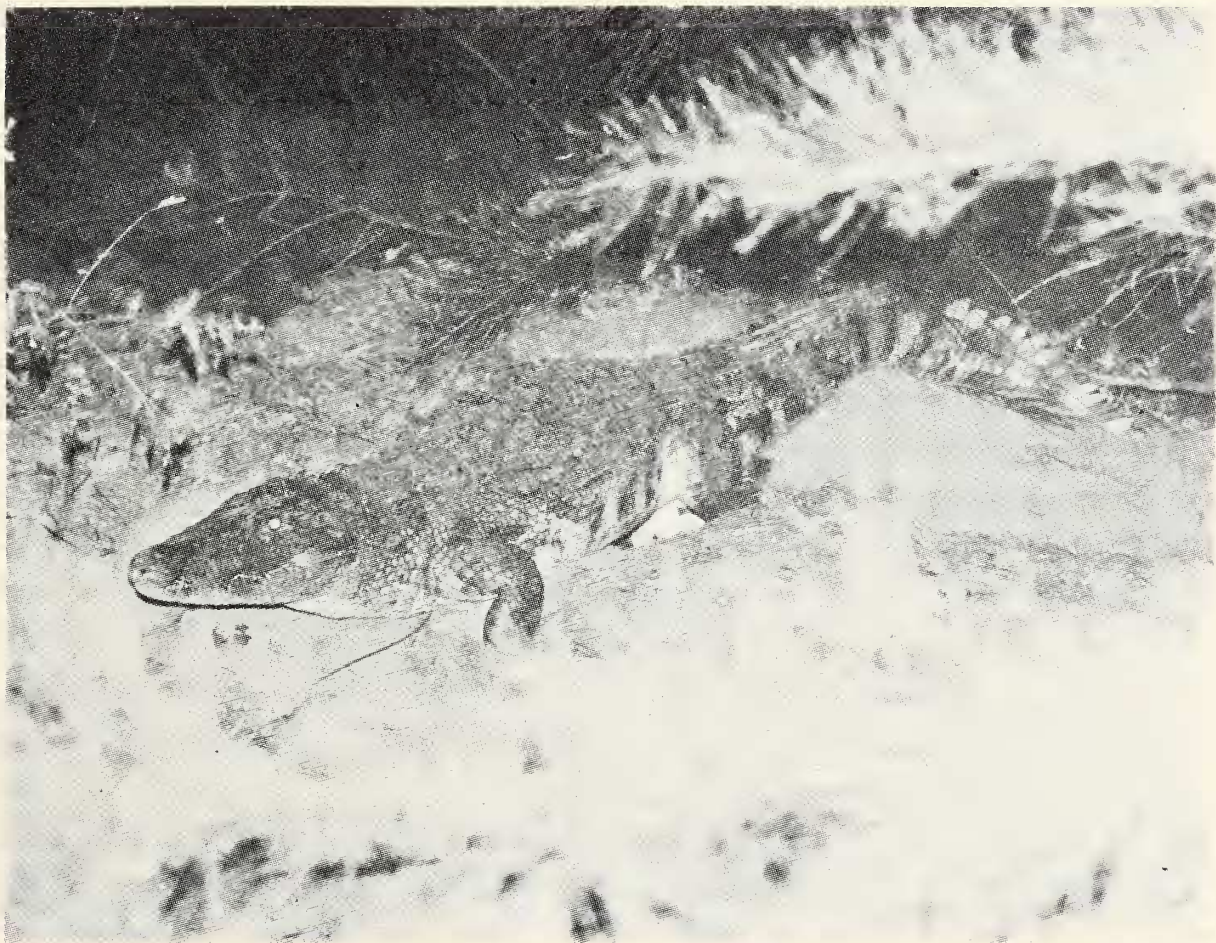
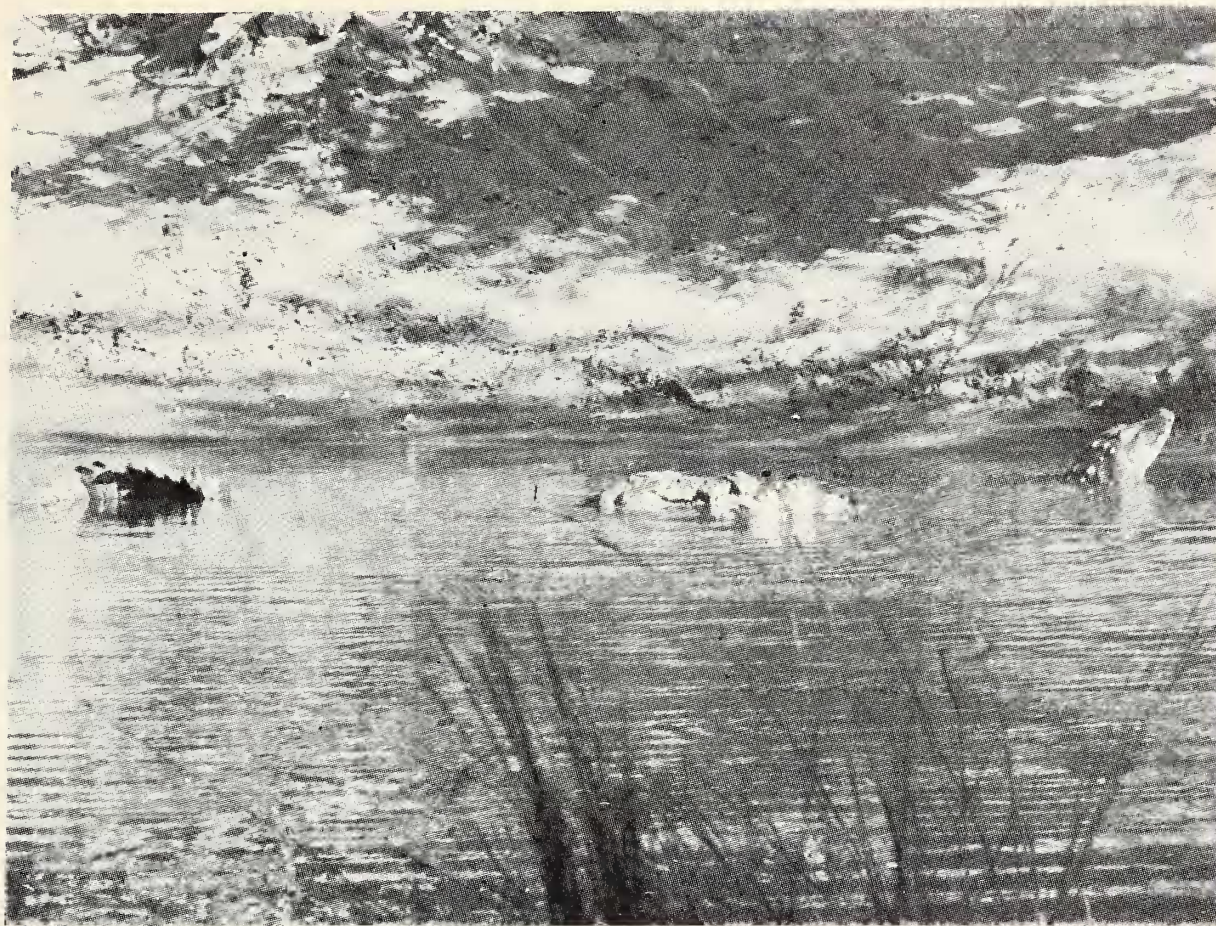


Fig. 3. Cross-section of mugger nest showing position of eggs before and after female shifts them with hind feet.

scratching with alternate movements of her hind legs, gently pushing sand into the nest hole. Sand was scraped over the nest and then periodically packed by treading with the hind feet (Figures 7 and 8). At 2210 she started turning on her nest, making seven full clockwise circles, completely flattening the nest area.

During wild egg collection programmes in 1975 and 1976, field study and surveys, over 50 wild nests were observed. Tables 5 and 6 give some of the physical characteristics of the nests. Hole length apparently corresponded to the length of the female mugger's hind leg. In most nests the soil at the egg cavity level was damp.

Locations included artificial reservoirs without shade, small, densely vegetated streams, and tidal lagoons (Whitaker and Whitaker 1975, 1979; Choudhury *et al.* 1979). At Amaravathi Reservoir the tracks of a mugger were followed into a hilly scrub forest over 1 km from the reservoir to where a 2.4 m female was found (Whitaker 1976 b). She later nested here (B.C. Choudhury, in litt.) but unsuccessfully, as the soil was too shallow. This



Above: Male mugger with arched tail approaches receptive female during courtship.

Below: Female mugger at Madras Crocodile Bank laying eggs.



Above: Female mugger scraping sand over nest site.
Below: Female mugger packs the finished nest by treading with hind feet.

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unusual nesting behaviour was postulated to be due to the excessive human disturbance in the area. (Before protection, 90% of the eggs were taken each season by herdsman and fire-

minutes. She finally appeared to notice Natesan's close presence and entered the water, watching from 10 m. out as the investigator checked the nest (Whitaker 1976 a).

TABLE 5
DATA ON 50 WILD MUGGER NESTS IN TAMIL NADU

Hole length (cms)	Hole width (cms)	Distance from water	Height above waterline (m)	Layer of sand/earth covering eggs (cms)
35-56	22:14-31	10 m:1 m-2 km	6.2:1.5-10	19.5:13-26

wood collectors). At Amaravathi, nine out of eleven nests were situated on slopes facing east.

At Amaravathi, Kilikudi and Sathanur trial nest holes were a common feature near nests. *C. palustris* usually digs one or more trial nest holes before the final egg chamber. At Vakkaramari a female was seen making a trial nest in daylight and 2-3 trial nest holes were found for each nest (Whitaker 1974).

TABLE 6

SOIL TYPE AND SHADE AT 59 WILD MUGGER NEST SITES (% NESTS)

Gravel/sand	Sand	Black clay	Loamy soil
37	34	17	10
Humus	Unshaded	Partly shaded	Fully shaded
1.7	86	7	7

An MSP investigator, V. Natesan observed a wild female mugger nesting at Vakkaramari, Tamil Nadu at 0630 on 15 March, 1976. She faced up the embankment and, eyes closed, made frequent straining movements as the eggs were deposited. She then started scraping soil forward with the front feet, turning while doing so. She continued scraping soil from the excavation back into the hole using her hind feet. She then flattened the site with her belly and lay still on the nest for a further fifteen

Clutch and egg size

Mugger lay 25-30 eggs; details of clutch sizes in different localities are given in Table 7. Clutch sizes were similar in north and south Indian nests. Although not adequately quantified it has been observed that clutch size is closely related to the size of the female. The average size of 340 eggs from wild nests in South India was 7.40 x 4.70 cms and weighed an average of 128 gms, closely corresponding to captive bred specimens eggs measured at MCB.

TABLE 7

CLUTCH SIZES OF MUGGER NESTS

Place	N	Clutch size x:range
Sathanur Reservoir, Tamil Nadu	5	27:17-35
Amaravathi Reservoir, Tamil Nadu	11	31:26-35
Vakkaramari, Tamil Nadu	3	32:18-46
Kilikudi, Tamil Nadu	3	19:16-21
MCB (8 females)	43	24: 8-39
MCB (1 female)	6	25: 8-33
Hiran Lake, Gujarat	2	25
Powai Lake, Maharashtra	1	17
Jaipur Zoo, Rajasthan	5	32:22-41
Total	79	26: 8-46

(Whitaker 1974, 1979 a, 1977; Whitaker and Whitaker 1975; 1977 b; Prakash 1971).

Incubation period and nest temperature

In captivity mating begins about two months before the first egg laying, suggesting a developmental period of 40-60 days. Incubation of mugger eggs averages about 2 months, details of captive incubated clutches are given in Table 8 which shows a slightly longer duration for nests in South India.

TABLE 8

INCUBATION PERIODS OF MUGGER NESTS

Place	N	Incubation
		period (days) \bar{x} : range
South India (wild)	20	67:41-80
South India (MCB)	33	68:41-85
North India (wild)	1	74
North India (Jaipur Zoo)	5	54:44-68

(Whitaker 1978, 1979 a, 1980; Whitaker and Whitaker 1975; Prakash 1971).

Nest temperatures in wild nests in South India ranged from 18°C in the early morning to 35°C in the early afternoon. In 1980 the overall nest temperature average at MCB was 31.3°C for the four months of February-May.

Nest losses

Of the 59 nests observed in the wild, 39% were collected for hatching in captivity, 36% were raided by humans for food, 15% hatched naturally, 3% spoiled, 5% were destroyed by predators and 1.5%, i.e. one nest, was destroyed by the female crocodile.

Multiple clutches per season

When double clutching was first observed at MCB in 1976 in a 19 year old female (Nova) it was thought to be exceptional or aberrant behaviour. Since then however, the

laying of two clutches per season has become the norm for 6 females. Table 9 illustrates the

TABLE 9

MUGGER DOUBLE CLUTCHING DATA AT MCB (MEANS FOR 1979 AND 1980 SEASONS)

N	\bar{x} clutch size A nests	\bar{x} clutch size B nests	$\bar{x}\%$ hatching success A nests	$\bar{x}\%$ hatching success B nests
22	29.2	23.6	59.1	47.0

N	\bar{x} incubation period A nests	\bar{x} incubation period B nests	\bar{x} no. days between A & B nests
22	65 days	70 days	41

(Whitaker 1980)

details of the multiple nesting which occurred in 1979 and 1980. Clutch size and hatching success were slightly lower in 'B' nests. 'A' nests took an average of 5 days less incubation time, corresponding to lower temperatures prevailing during the 'B' nest incubation period. (Fig. 4).

Double clutching at MCB may be a result of the combination of high temperatures and high feeding rates. There seem to be three possibilities which might explain the phenomenon :

- a) single mating with arrested development of second clutch
- b) single mating and storage of sperm
- c) double mating.

Sporadic mating of mugger was observed late in the season (March/April) but no peak similar to the December activity was noted. While the period of egg development in first and single clutches appears to be about 60 days there was an average of only 41 days between first and second nests. There is no

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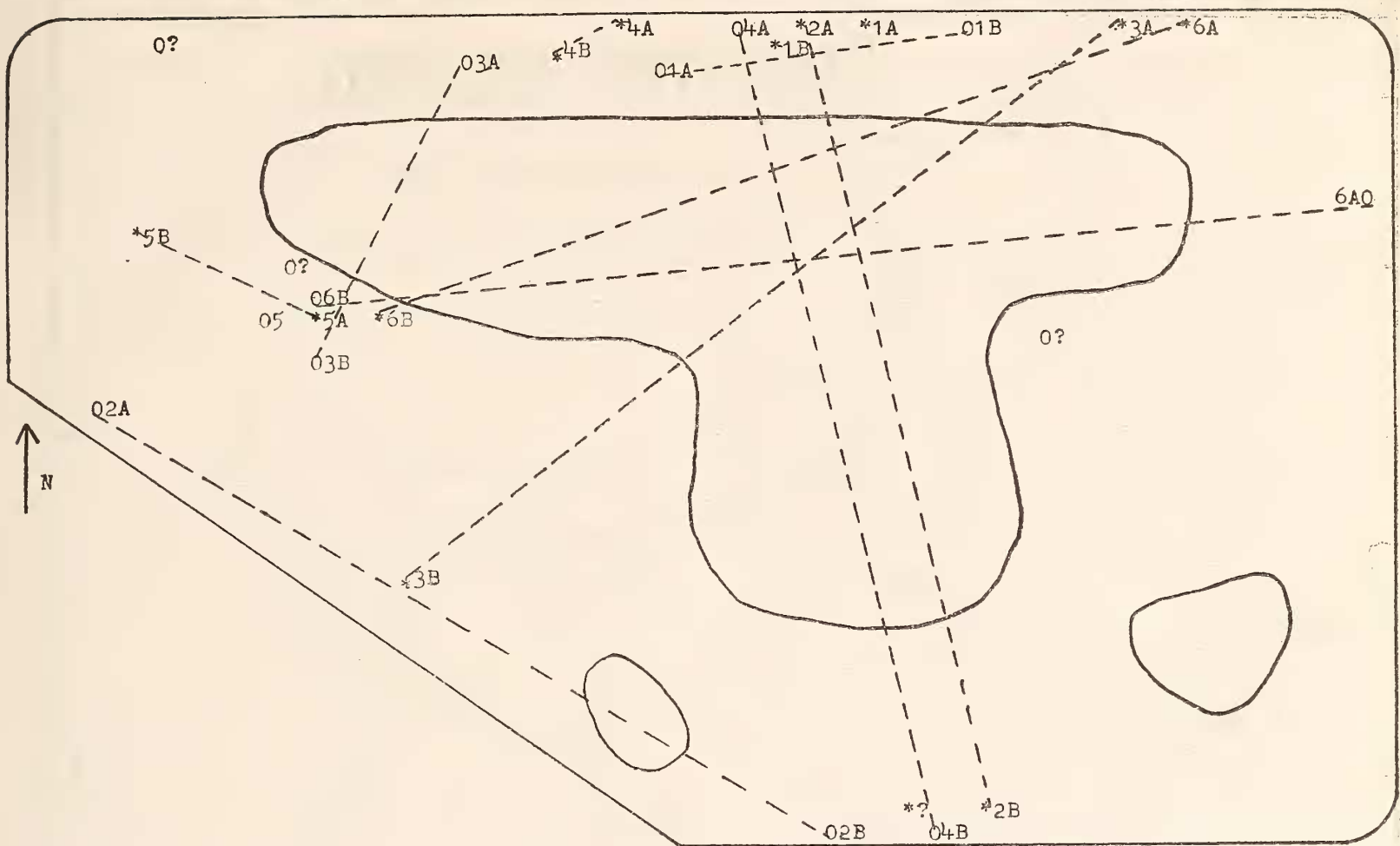


Fig. 4. Nest site selection by double clutching mugger in the Madras Crocodile Bank breeding enclosure. Dotted lines illustrate the tendency for widely separated site selection by individual females.

evidence of double clutching in wild mugger. Tribal inhabitants of crocodile habitat have generally proved to be the most reliable informants on mugger habits and only once have these egg collectors (Poliyars at Amravathi Reservoir) indicated that they had seen fresh nests later than the normal season. The implications of double clutching for commercial farming are obvious, whether it could be of some survival value for wild mugger is a matter for conjecture. The mean distance between A and B nests was 22.5 m, while nests of different females averaged only 5 m apart (Table 10).

Messel (pers. comm.) suggests that 'early' and 'late' nests of *C. porosus* in Australia may be first and second nests of the same animal.

Graham (1968) noted that over 50% of mature male *C. niloticus* had motile semen for 6 months. In addition, 24% of females had two or more sets of enlarging ovarian follicles of greatly differing sizes. He suggests that maturation of one set of ova may be accompanied by development of another set, resulting in the production of two batches of eggs in one season. Graham's conclusion is that "the time sequence of events would permit an animal to breed twice." According to Cott (1961), fresh crocodile eggs were found during two periods of the year in northern Lake Victoria (Uganda): August and early September, and again in December and January.

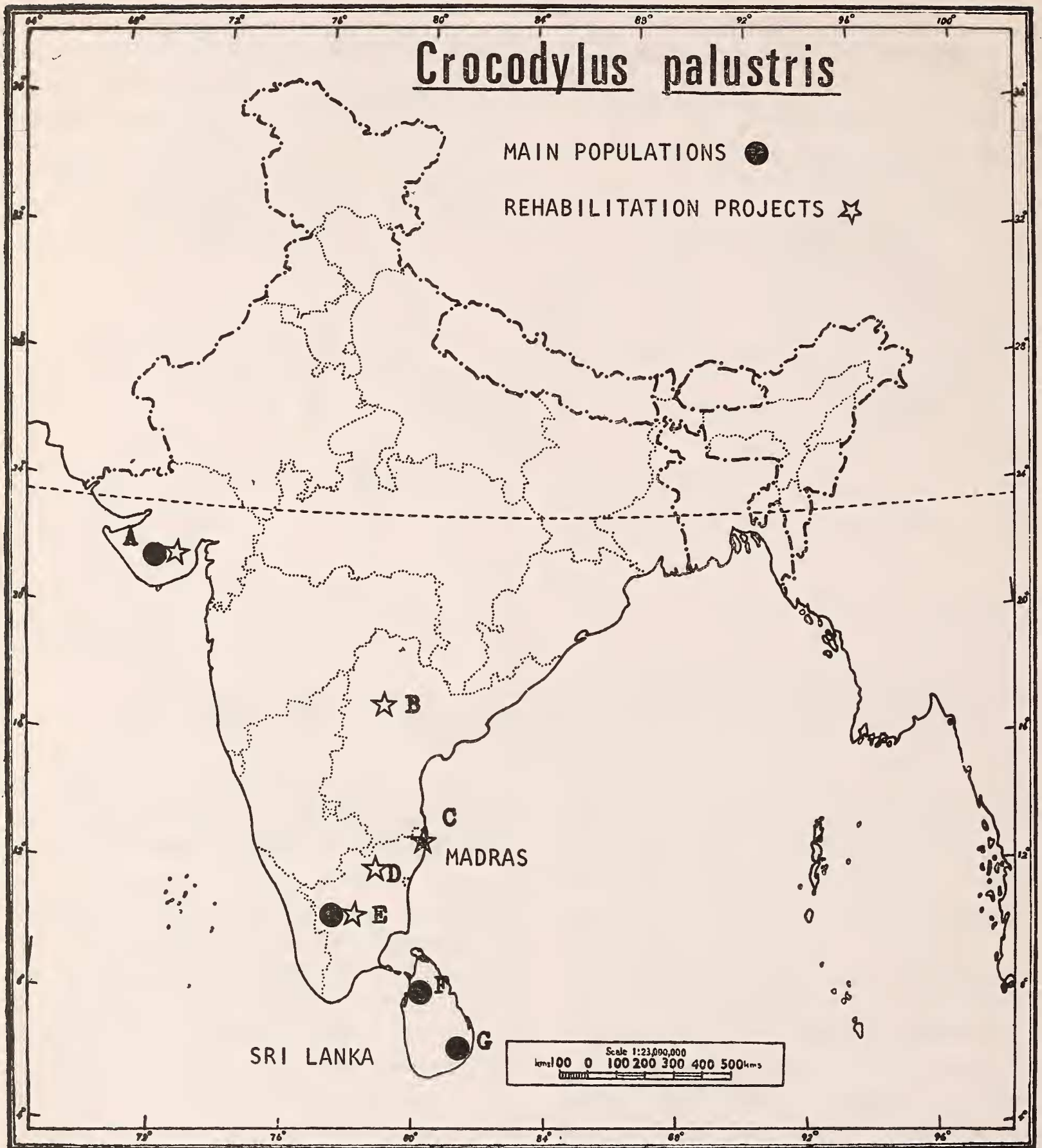


Fig. 5. Main *Crocodylus palustris* populations and projects.
A. Gir National Park, Gujarat. B. Hyderabad, Andhra Pradesh. C. Madras Crocodile Bank, Tamil Nadu. D. Sathanur reservoir, Tamil Nadu. E. Amaravathi reservoir, Tamil Nadu. F. Wilpattu National Park, Sri Lanka. G. Yala National Park, Sri Lanka.

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Protection of nest

Nest defence has been observed both in the wild (S. Valliappan, pers. comm.) and in captivity (Whitaker and Whitaker 1977 a). At MCB and MSP nesting females defended nest sites and adjacent water areas and engaged in threat displays. They often thrashed their tails from side to side and made repeated serious charges at intruders, both crocodilian

TABLE 10

DISTANCES BETWEEN NESTS OF DOUBLE CLUTCHING MCB MUGGER

No.*	Female	1979	1980
		Distance from A to B nest (m)	Distance from A to B nest (m)
1.	Karruppukann	1.90	17.40
2.	Chitra	32.00	9.50
3.	Stumpy	48.50	20.50
4.	Vijaya	5.80	32.00
5.	Nova	7.00	—
6.	Chidambaram	38.20	34.00
	<i>Range and average</i>	<i>Range and average</i>	
	1.90-48.50:22.23	9.50-34.00:22.70	
	Distance to nearest nest (m)	Distance to nearest nest (m)	
	<i>Range and average</i>	<i>Range and average</i>	
	0.75-11.90: 3.57	1.00-20.45: 6.61	

* refers to map of MCB mugger breeding enclosure, Figure 4.

and human. If undisturbed the female will spend most of the incubation time at her nest and in the water near by. One female (Nova) fasted throughout incubation, while other younger females were less attentive to nests and did not fast.

The role of the male *C. palustris* in nest protection has not been clearly established. A male at Ahmedabad Zoo ignored the female after copulation (David 1970). Similarly Yadav (1969) negates participation of the male in

nest protection and defence of young. The male *C. niloticus* takes part in nest excavation and hatchling transport (Pooley 1974) as does the New Guinea crocodile (Lang, in press).

Hatching, release and transport of young

The female at MSP was observed at 0100 on 22 May 1978 excavating her nest with her front feet and head, leading 6 hatchlings to the pond 6 m, away, and communicating with them through grunts. She later excavated 5 more young. The female and hatchlings were heard calling sporadically all night up to 0500 (Whitaker 1980).

At 0900 the female chased the keeper from the enclosure. She pushed hatchlings out on to the palm leaves outside the pool with her snout. RW picked up a hatchling and on hearing its distress cry the female charged and bit the tree behind which he stood.

At 0950 the male was with the hatchlings in the main pond and the female in the adjacent pond. The female picked up a hatchling in her mouth and carried it to the main pond, shaking it out of her mouth where the other hatchlings were grouped (J. Vijaya, pers. comm.).

At 1010 she went again to her nest (possibly in response to a call) and dug with her front and (less often) hind feet. She moved clockwise over her nest, sometimes putting her nose in and biting clods of earth.

An egg was removed with the jaws, jerked back, and gently punctured by the front teeth. The hatchling slipped into the buccal pouch, squirming. She brought it, tail visible between her teeth, to the pond. It was observed that the hatchlings spent the first day almost entirely on dry land.

At 1100 another hatchling was picked up at the nest and brought to the same spot next to the pond.

Bone (1943) reports hearing baby mugger calling for "several days" from inside a nest. Neill (1971) reports that the grunt or distress cry of a juvenile will summon an adult but dismisses as folklore the idea that the mother crocodile responds to the call of the hatchlings and digs them out. Campbell (1973) discusses the probable significance of hatchling vocalization and its importance in attracting the mother at hatching time.

TABLE 11

VERNACULAR NAMES OF MUGGER

Language	Place	Vernacular name(s)
Urdu	Pakistan	Baghori, maggar
Hindustani	North India	Maggar mach
Bihari Hindi	Bihar	Bocha
Bengali	West Bengal	Kumeer
Tamil	Tamil Nadu	Mothalay
Telugu	Andhra Pradesh	Mosalay
Kannada	Karnataka	Mosalay
Singhalese	Sri Lanka	Hale kimbula, gette kimbula

Creche formation and defence of young

At MSP 13 hatchlings remained in the group or creche initially formed by the female for two months. They stayed with the male and female for 12 months through the next breeding season and no aggression toward the young on the part of either was observed. Groups of hatchlings were reported several times by fishermen and others and one creche group of 17 mugger hatchlings was found at Kedarhalla (Whitaker and Whitaker 1976).

At MCB during capture of hatchlings from an undetected nest, a mature male and female and a sub-adult male made repeated lunges and charges at the keepers and demonstrated a fierce defence of the hatchlings.

Both females and males respond to the juve-

nile distress cry. At MSP a hatchling was held near the enclosure and its distress cry brought a female charging out of the water and almost over the 1.5 m wall. Wild mugger, apparently of both sexes, responded to mimicked distress cries by approaching, leaving the water and charging.

Reddy (1978) reports 15 hatchlings eaten by the parent male and female at Indira Gandhi Zoological Park. This behaviour could have resulted from stress in confined quarters.

Conservation

MCB has been established with help from the World Wildlife Fund, New York Zoological Society, Tamil Nadu State Government, West German Reptile Leather Association and MSP Trust. It is self sustaining by tourism, and is a trust for the breeding, rearing and supply of live crocodiles for restocking and captive breeding programmes in India. Since its beginning in 1974 the Bank has accumulated breeding stock from captive sources, reared 250 mugger from wild collected eggs and produced 1100 mugger from captive breeding. 500 juvenile mugger (mostly one to two year old) have been supplied to several state governments for rearing and/or release.

The UNDP /FAO/Government of India crocodile programme has resulted in the formation of 10 protected habitats specifically for crocodilians, with 4 states involved in egg collection, rearing and release projects. At present about 800 mugger are being reared for release mainly in Tamil Nadu, Gujarat and Andhra Pradesh. To date about 650 have been released in separate habitats.

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